

Genera of American Strombid Gastropods (Gastropoda: Strombidae) and Remarks on Their Phylogeny

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Abstract. *Persististrombus* gen. nov. is created to accommodate a number of fossil and one Recent species which form a distinct lineage starting in Early Oligocene of Europe with *Strombus radix* Brongniart, 1823, via the Oligocene to early Miocene *S. bonellii sensu stricto* Brongniart, 1823 and a number of Caribbean extinct species to the Recent Panamic faunal province *Strombus granulatus*. The genus level name *Lobatus* Iredale, 1921 (type species *bituberculatus* Lamarck, 1822) is available. Possible relationships between *Persististrombus* gen. nov. and other Caribbean and Panamic Strombidae are discussed but remain uncertain as the phylogeny of these species is not fully elucidated. Putative evolutionary scenarios are briefly considered.

Gastropoda, Strombidae, new genus, *Persististrombus*, *Lobatus*, phylogeny

INTRODUCTION

The discovery of aberrant specimens of the well known *Strombus granulatus* Swainson, 1821 from the Islas Galápagos and Isla del Coco discussed by Kronenberg & Lee (2004) combined with an earlier paper by Lozouet & Maestrati (1986) compelled the authors to further investigate the relationships of this species and the fossil record of its relatives.

Strombus granulatus was assigned to *Lentigo* Jousseaume, 1886 by Abbott (1960), and this allocation was followed by subsequent workers like Walls (1980), Kronenberg and Berkhout (1984), and DeTurck *et al.* (1999).

As indicated before (Kronenberg & Vermeij, 2002), the lines between subgenera as recognized by Abbott (1960) are rather blurred and arbitrary. *Lentigo*, to which Abbott (1960) assigned five species, *viz.* *Strombus lentiginosus* Linnaeus, 1758 (type species TS); *S. pipus* (Röding, 1798); *S. fasciatus* Born, 1778; *S. latus* Gmelin, 1791; and *S. granulatus*, is an example of this problem. On the basis of shell characters there are at least three supraspecific taxa included in this group. Moolenbeek & Dekker (1993) have already allocated *S. fasciatus* to *Conomurex* Fischer, 1884 based on shell morphology and characters of the radula. Subsequently, DeTurck *et al.* (1999) replaced it in *Lentigo* without comment. Kronenberg & Vermeij (2002) indicated that both *Strombus granulatus* and *S. latus* differed in a number of conchological characters from the Indo-

Pacific *Lentigo lentiginosus* and *L. pipus*. More recently it has been demonstrated, based on anatomical characters (Simone, 2004) and molecular sequence data (Latiolais, 2003 and Latiolais *et al.*, 2006), that the genus *Strombus sensu* Abbott is not monophyletic.

Sacco (1893:12) was the first to recognize a lineage from the fossil *S. radix* Brongniart, 1823 and *S. bonellii* Brongniart, 1823, for which *Strombus nodosus* (Borson, 1820) might be an earlier name, see Sacco (1893:4) of the Recent *S. granulatus*, an opinion followed by Lozouet and Maestrati (1986). This was acknowledged by Jung & Heitz (2001), who described a number of fossil species, allocating those to *Lentigo*. They also included the Recent *Strombus raninus* Gmelin, 1791, a species previously assigned to *Tricornis* Jousseaume, 1886 or, more recently, to *Lobatus* Iredale, 1921 (Petuch, 1994).

Consistent with reasoning of Kronenberg & Vermeij (2002) and data presented by Latiolais (2003), Simone (2004), and Latiolais *et al.* (2006), and to accommodate the lineage of the Early Oligocene species of Europe and a number of fossil species described by Jung & Heitz (2001) to the Recent *S. granulatus*, a new genus is described herein. As Jung & Heitz (2001) argued that the name *Lobatus* Iredale, 1921 is unavailable, we discuss the nomenclatorial status of that taxon. A review of the literature for possible relationships between the new genus described herein and other strombid genera revealed that there is a number of possible relationships between the Recent Western

Atlantic and Panamic Province fauna and fossil species known from the Early Oligocene to Early Miocene of Europe. These are discussed briefly.

Strombus albirupianus Dall, 1890, described from the Late Eocene (Jackson) white limestone overlying the Claiborne sands, Claiborne Bluff, Alabama, does not appear to be closely related to this lineage judging from the description and figures by Dall (1890:174–175, pl. 12 figs. 2, 10) and is not considered here.

Likewise, two other American fossil strombid species, *S. liocyclus* Dall, 1915 from the Miocene Tampa silex beds, Ballast Point, Tampa Bay (Florida, USA) [*vide* Boss *et al.*, 1968] and *S. leurus* Woodring, 1928 from the Pliocene Bowden Formation of Jamaica are not discussed here as they apparently left no Recent descendants in the Americas. *Strombus liocyclus* was allocated to *Canarium* Schumacher, 1817 by Abbott (1960:63). *Strombus leurus* was not discussed by Abbott, but the species bears a strong resemblance to species allocated to *Dolomena* Wenz, 1940 [*Dolomena* Iredale, 1931 is not available; see Kronenberg & Dharma, 2005 and references therein] (Woodring, 1928:326–327; pl. 24, figs. 3–5).

Another possible clade, consisting of the genus *Orthaulax* Gabb, 1873 (*O. inornatus* Gabb, 1873), known from the lowermost middle Eocene of Italy (*O. dainellii* Savazzi, 1989) with a number of Oligocene and Miocene species in America (see Vokes & Vokes, 1968 for a review and discussion) is not discussed herein as we think that *Orthaulax* is not closely related to the Recent American species.

Further, a number of fossil strombid species are known from South America, dating as far back as the Eocene. These have been allocated to various (sub)genera, like *Oostrombus* Sacco, 1893 (type species *Strombus problematicus* Michelotti, 1861) but are probably not closely related to the Recent species and may belong to another clade which has become extinct.

SYSTEMATICS

Family Strombidae Rafinesque, 1815

Persististrombus Kronenberg and Lee *gen. nov.*

Type species: *Strombus granulatus* Swainson, 1822 Pliocene to Recent

Description: Shell of moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch elongate and conical with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate.

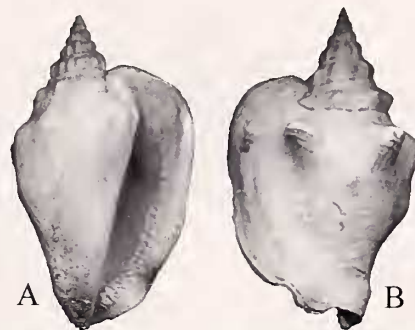


Figure 1. *Persististrombus aldrichi* (Dall, 1890). U.S.A., Florida, Calhoun Co. Chipola River just above Farley Creek Chipola Formation, Early Miocene. Leg. C. Hertweck, collection H. G. Lee. Actual size 47.9 mm. A. Apertural view, B. Dorsal view. Photos H. G. Lee.

Derivation: Derived from the Latin *persistens* (persistent) combined with *Strombus*, as the general shell morphology of species assigned to this genus has remained almost unchanged from the Early Oligocene (Lozouet & Maestrati, 1986) to Recent. The late Eocene record by Lozouet and Maestrati (1986) for *S. radix* may be erroneous (personal communication Lozouet to GCK, January 2007).

Other species assigned to *Persististrombus* *gen. nov.* are: *Strombus aldrichi* Dall, 1890 from the early Miocene of the Chipola Beds, Florida, U.S.A. (Figure 1); *S. baltrae* García-Talavera, 1993 from the Pliocene of Isla Baltra, Islas Galápagos; *S. barrigoniensis* Jung & Heitz, 2001 from the Cubagua Formation, early Pliocene of Venezuela; *S. bonellii* Brongniart, 1823 from the Early Miocene of France (Figures 2, 3) [this may be a junior synonym of *S. nodosus* Borson, 1820, *vide* Sacco (1893:4)]; *S. insulanus* Jung & Heitz, 2001 from the Escudo de Veraguas Formation, middle Pliocene of Panama; *S. mardieae* Petuch, 2004 from the early Miocene of the Chipola beds, Florida, U.S.A.; *S. obliteratedus* Hanna, 1926 from the Pliocene of Imperial County, California, U.S.A.; *S. radix* Brongniart, 1823 from the Early Oligocene of Europe (Figure 4); *S. toroensis* Jung & Heitz, 2001 from the Cayo Agua Formation, early Pliocene of Panama; a radiation of the Middle Miocene of Europe (Harzhauser & Kronenberg in prep.) and a number of species reported by Jung & Heitz (2001) which are identified by means of open nomenclature or by letters. Powell (1988:17) also listed a – possibly new – species which he allocated to *Strombus* (*Lentigo*), but specimens of it haven't been examined by us. This species is not unlikely a *Persististrombus* as well. We agree with Jung & Heitz (2001:28) that *S. granulatus cortezianus* Durham, 1962 [new name for *S. granulatus acutus* Durham, 1950 *non* G. Perry, 1811] is a synonym of *S. granulatus*. For an overview of species allocated to



Figure 2. *Persististrombus bonellii* (Brongniart, 1823). France, Dept. Gironde, Le Peloua. Burdigalian, Early Miocene. Leg. B. Landau, collection B. Landau. Actual size 86.8 mm. A. Apertural view, B. Apical view, C. Dorsal view. Photos B. Landau.

Persististrombus gen. nov. through time and space, see Table 1 and Figure 5.

Although *Persististrombus* gen. nov. has a number of characters in common with *Lentigo* Jousseaume, 1886 (TS by monotypy: *Strombus lentiginosus* Linnaeus, 1758), there are conspicuous differences: in *Lentigo* the adapical part of the outer lip has two notches, resulting in two lobes, of which the most adaxial one is attached to the spire of the shell; species assigned to *Lentigo* have



Figure 3. *Persististrombus bonellii* (Brongniart, 1823). France, Dept. Gironde, Le Peloua. Burdigalian, Early Miocene. Leg. B. Landau, collection B. Landau. Actual size 83.0 mm. A. Apertural view, B. Dorsal view. Photos B. Landau.



Figure 4. *Persististrombus radix* (Brongniart, 1823). France, dept. Landes, Espibos, Gaas. Chattian, late Oligocene. Leg. B. Landau, collection B. Landau. Actual size 64.0 mm. A. Apertural view, B. Apical view, C. Dorsal view. Photos B. Landau.

a more distinct posterior canal, a number of small triangular extensions at the abapical side of the outer lip on the flange between the stromboid notch and the anterior canal, very often rather worn in *L. lentiginosus*, and a columellar callus which does not reach the base of the columella, but is thickened at its abapical part, but not forming a distinct pad as in some species of *Euprotomus*. Species assigned to *Persististrombus* gen. nov. also have a relatively higher spire than do species of *Lentigo*, but within *Persististrombus* gen. nov. species with a low spire do occur (Harzhauser & Kronenberg, in prep.). *Lentigo* is here considered to be restricted to the Indo-Pacific; see also Kronenberg & Vermeij (2002). *Persististrombus* gen. nov. has many characters in common with *Strombus* Linnaeus, 1758 (type species by SD Montfort, 1810: *Strombus pugilis* Linnaeus, 1758), especially the spire. Differences between *Persististrombus* gen. nov. and *Strombus* are more difficult to quantify, and are more qualitative. In *Strombus* the tips of the shoulder knobs are pointed whereas in *Persististrombus* gen. nov. these tips are usually rounded. But the population of *P. granulatus* from the Islas Galápagos has the tips of the shoulder knobs, better referred to as spines, pointed. In *Strombus* there is no sculpture in the form of knob-like structures abapical of the row of these shoulder knobs. In *Persististrombus* gen. nov. there usually are one or sometimes two of such rows, but in the middle Miocene of Europe there is at least one species of *Persististrombus* gen. nov. which only has the shoulder knobs present, and again the population of *P. granulatus* from the Islas Galápagos does not have

Table 1
Distribution in time and space of *Persististrombus* gen.nov. species.

Species	Age	Locality
<i>P. radix</i>	Oligocene	Mediterranean region
<i>P. bonellii</i>	early Miocene	Mediterranean region
<i>P. aldrichi</i>	early Miocene	Florida, U.S.A.
<i>P. mardia</i>	early Miocene	Florida, U.S.A.
<i>P. spp.</i> Vienna basin	early middle Miocene	Vienna Basin, Austria
<i>P. cf. insulanus</i>	early middle Miocene	Grenadines
<i>P. sp. C</i> (Jung and Heitz)	middle – late Miocene	Venezuela
<i>P. sp. A</i> (Jung and Heitz)	late Miocene	Venezuela
<i>P. barrigonensis</i>	early Pliocene	Venezuela
<i>P. toroensis</i>	early Pliocene	Panama
<i>P. sp. E</i> (Jung and Heitz)	early Pliocene	Jamaica
<i>P. insulanus</i>	middle Pliocene	Panama
<i>P. obliteratus</i>	Pliocene	California, U.S.A.
<i>P. sp. B</i> (Jung and Heitz)	Pliocene	Panama
<i>P. baltrae</i>	Plio-Pleistocene	Islas Galápagos
<i>P. granulatus</i>	late Pliocene – Recent	Panamic fauna province
<i>P. sp. D</i> (Jung and Heitz)	Pleistocene	Panama

a second or third row of knobs present in all specimens (Kronenberg & Lee, 2005). Fossil species of *Strombus* s.s. may have spiral sculpture (e.g., *Strombus lindae* Petuch, 1991; see Petuch 1994: pl. 21, fig. A) as grooves on the body whorl. But also the “nicaraguensis” form of *Strombus pugilis* (see Clench & Abbott, 1941: pl. 6) has this kind of spiral sculpture on (part of) the body whorl. In *P. aldrichi* this sculpture, though less conspicuous, is present, but the abapical part of the

body whorl is never smooth as in *Strombus*. In *Strombus* the outer lip is more widely expanded than in *Persististrombus* gen. nov., and the adapical aspect of the outer lip (wing) is more or less pointed (not very evident in all specimens of *S. alatus*). This outer lip expansion is particularly evident in the apical view: In *Strombus* the labrum arches ventrally from its posterior origin at the suture so as to form a large open sinus with its free margin directed abaxially, whereas that

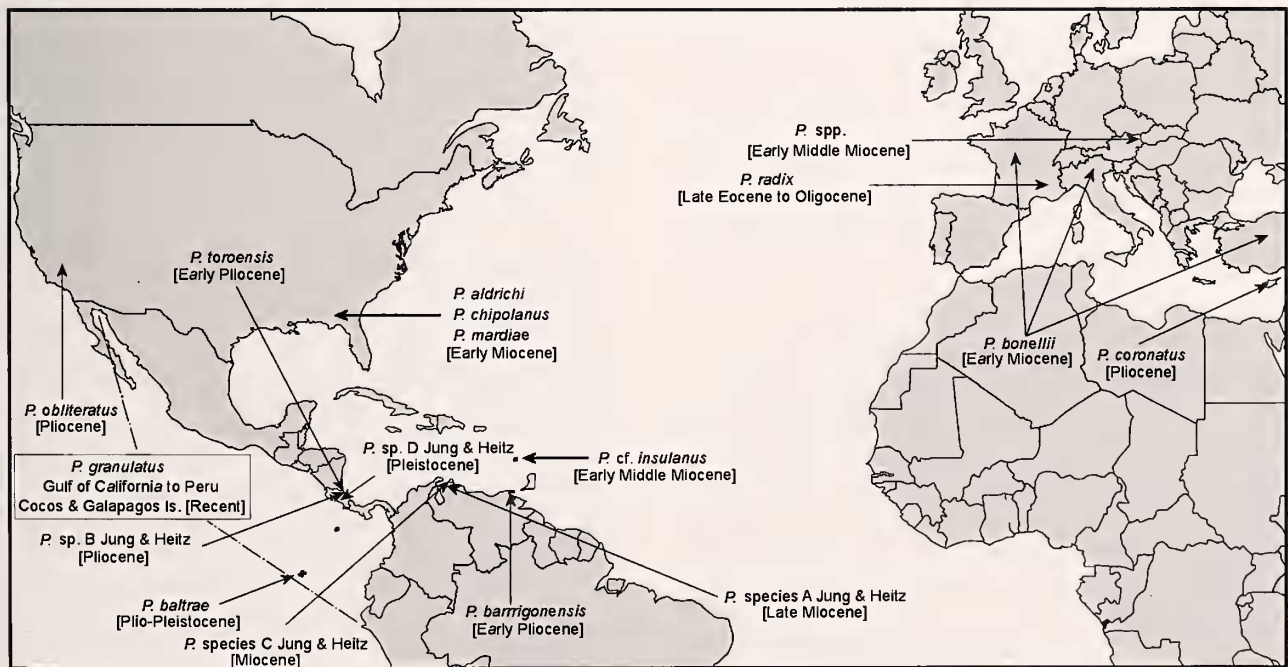


Figure 5. Geographic and Stratigraphic Distribution of *Persististrombus* gen. nov. species.

Table 2

Summary of distribution and characters of *Lentigo*; *Persististrombus* gen. nov.; *Strombus*; and *Lobatus*.

	<i>Lentigo</i>	<i>Persististrombus</i>	<i>Strombus</i>	<i>Lobatus</i>
Zoogeographical province	Indo-Pacific	Parathetys – Caribbean – Panamic	Caribbean – Panamic	? Parathetys – Caribbean – Panamic
Tip of shoulder knobs	rounded	rounded	pointed	rounded
Knobs abapical of shoulder knobs	present	usually present	absent	usually absent
Spiral grooves in adult species	absent	absent	absent or present	present
Outer lip	slightly expanded	slightly expanded	clearly expanded	clearly expanded
Transition lateral part outer lip to adapical part outer lip	rounded	rounded	pointed; not always clear in <i>S. alatus</i>	Variable, from rounded to pointed, but when pointed forming a distinct groove from tip of point into the aperture
Abapical part of outer lip	bilobed	simple	simple	simple
Triangular projections between strombid notch and anterior canal	present	absent	absent	absent
Columellar callus	thickened abapical	not thickened	not thickened	not thickened

aspect of *Persististrombus* shows a narrower sinus which tends to curve adaxially at its free margin. Juveniles of *P. granulatus* (see e.g., Emerson & Old, 1963:8 fig. 7) have a distinct spiral sculpture, a character which they share with *Strombus*. *Strombus* is restricted to America, and it may have been derived from a species of *Persististrombus* gen. nov.

Persististrombus gen. nov. differs from other American species, here assigned to *Lobatus* Iredale, 1921, in rate of expansion of the outer lip and sculpture of the body whorl. Several genus level taxa for these American species are available, viz. *Aliger* Thiele, 1929 (TS *Strombus gallus* Linnaeus, 1758); *Eustrombus* Wenz, 1940 (TS *Strombus gigas* Linnaeus, 1758); *Macrostrombus* Petuch, 1994 (TS *Strombus costatus* Gmelin, 1791); and *Titanostrombus* Petuch, 1994 (TS *Strombus goliath* Schröter, 1805 [not 1905 (Petuch, 1994:261), an apparent *lapsus calami*]). The relationships within these American species are still unclear, and whether these should be regarded as subgenera of *Lobatus* is beyond the scope of the present paper; see table 2.

Persististrombus granulatus occurs from the northern end of the Gulf of California (Sea of Cortez) to Ecuador (Keen, 1971:421). Skoglund (2002:55) added some records to the known distribution, including Isla Gorgona (Colombia) and Islas del Coco (Costa Rica) southward to Zorritos, Perú. Finet (1994) listed Islas Galápagos and provided other references in support.

Given the rather aberrant shape of some of the specimens originating from the Islas Galápagos in comparison to the continental specimens of *P. granulatus*, we believe a process of speciation of the Galápagos population is emerging. This speciation may, however, be frustrated by an infrequent influx of

larvae originating from the continental population. It seems that there is a genetic factor involved in the various insular populations' phenotypy. There may even be significant segregation of genomes among populations of *P. granulatus* (s.l.) by island or group of islands in the Galápagos. The islands may be the metaphorical battlefield for the (genetic) independence of the earlier immigrant waifs [as in the Isla Santa Fé morphs, see illustrations in Kronenberg & Lee (2004)]. However, at present we see no constant difference in characters of the shells to make a clear conchological separation among populations. We are aware that there is no proof for this hypothesis, and therefore this is highly speculative at present. However, this hypothesis can probably be tested by molecular analysis.

A NOTE ON *LOBATUS* IREDALE, 1921

Jung and Heitz (2001:48–50, fig. 26) described *Strombus fetus* from the Escudo de Veraguas Formation (late Pliocene) of Panama and assigned this species to the subgenus *Lentigo*. They based their description on only one specimen and stated that this species is not related to any of the species they studied, stating that *S. fetus* resembles *S. raninus* Gmelin, 1791 only superficially. They mentioned only one difference, viz. the size of the knobs on the shoulder of the body whorl. Indeed, most specimens of the Recent *S. raninus* have two large, spine-like knobs on the shoulder of the body whorl, which character is expressed in the nomen *S. bituberculatus* Lamarck, 1822, a synonym. Yet this is not always the case. In the private collection of the first author there are two specimens, viz. one from Aruba, Paardenbaai, inside reef in seaweed field, leg. Jan Berkhout, 1967 (GCK 5419); one from Aruba, Secoe di

Palma, *leg.* Jan Berkhout, 1968 (GCK 5423) in which the two last knobs on the shoulder of the body whorl are only slightly enlarged and one specimen from Panama, Isla Bastimentos, Bocas del Toro, found dead in surf zone, *leg.* Monika Forner, 30 November 1997 (GCK 5858) in which the development of the shoulder knobs is not different from *S. fetus* as illustrated by Jung & Heitz. After studying the description and illustrations, we regard *Strombus fetus* as a synonym of *S. raninus*, which may also be true for *S. praeranus* Kronenberg & Dekker, 2000 [new name for *Strombus wilsonorum* Petuch, 1994 *non* Abbott, 1967] and *Strombus magolecciai* Macsotay & Villaroel, 2001.

Petuch (1994) named a number of fossil Caribbean strombid taxa, both at the genus and species level. For *Strombus raninus*, Petuch used the subgenus name *Lobatus* Iredale, 1921. Jung and Heitz (2001:40) criticized the use of the name *Lobatus* by Petuch because the introduction of *Lobatus* was an historical accident, referring to Abbott (1960:53). However, the introduction of *Lobatus* by Iredale (1921:208) meets the requirements of the ICZN (Article 12.2.5), and therefore the name *Lobatus* Iredale, 1921 (TS *Strombus bituberculatus* by monotypy) is available.

POSSIBLE PHYLOGENIES OF RECENT AMERICAN STROMBIDS

Kronenberg & Vermeij (2002:53) argued that the Recent Western Atlantic and Panamic strombids (including the West African *Strombus latus* Gmelin, 1791, and excluding the Indo-Pacific *Gibberulus gibbosus* (Röding, 1798) which was reported by Mienis (1978) from the Islas Galápagos [as *Strombus* (*Gibberulus*) *gibberulus gibbosus*]), are monophyletic. This may be true because we have not been able to trace any fossil evidence of any *Strombus* (s.l.) in the Western Atlantic fossil record before *Persististrombus* gen.nov. made its appearance there.

Within this possible clade a number of groups (based on overall shell characters, and for which genus-level names are available; see above) can be discerned, *viz.*: *S. costatus*; *S. gigas*; *S. raninus* + *S. peruvianus* + *S. gallus*; *S. goliath* + *S. galeatus*. It should be noted here that in the analysis of stromboidean genus-level taxa, based principally on anatomical characters, Simone (2004) puts *Strombus raninus* (allocated to *Tricornis* by Simone) apart from the other American strombid species, i.e., branching off before *Lambis*, while all other American strombid species (as far as examined by Simone) branch off after *Lambis*.

Some possible scenarios for a phylogeny of the American species can be taken into consideration. With no pretense to an exhaustive presentation, we mention a few such, which can be tested using molecular data.

Scenario 1)

All recent American species are descendants of a species which is also ancestral to the recent *P. granulatus*. This may have happened in one single wave (that is that one species of *Persististrombus* is ancestral to all western Atlantic and Panamic Recent species) or in two (or more) waves in which one of these waves ended up in *S. pugilis*, *S. alatus* and *S. gracilior*; the other(s) resulted in all other species. Based on the molecular data as presented by Latiolais *et al.* (2006) this scenario of two waves seems most likely.

Scenario 2)

Sacco (1893:12) postulated that the late Miocene to late Pliocene *Strombus coronatus* De France, 1827 (from the Tortonian through Piacenzian of Europe) is ancestral to both the Recent West African *Strombus latus* (as *Strombus bubonius* Lamarck, 1822) and the Recent *Strombus costatus* (as *Strombus accipitrinus* Lamarck, 1822). All three of these species are extremely variable (see for *Strombus* (s.l.) *coronatus* e.g., Sacco, 1893, pl. 1, for *Strombus* (s.l.) *latus* DeTurck *et al.* pls 102, 103 and for *Strombus* (s.l.) *costatus* DeTurck *et al.* pls 43, 44), and a large number of names are available, especially for *S. coronatus*; see Sacco (1893).

Beneventi & Piccoli (1969), based on a number of fossil species, elaborated on this scenario and concluded that many Recent species descend from a lineage started by *Strombus fortisi* Brongniart, 1823 through *S. radix* and *S.* (s.l.) *coronatus*, to Recent Western Atlantic and Panamic province species, but also to Recent Indo-Pacific species assigned to *Euprotomus* and *Lentigo*. [The evolution of *Persististrombus* in Europe, except for *P. radix* and *P. bonellii* will be discussed elsewhere (Harzhauser & Kronenberg, in prep.)]. In their tree (Beneventi & Piccolo, 1969:17) *Persististrombus granulatus* also descended from *Strombus coronatus*, contrary to the results as shown by Jung & Heitz (2001) and our view. Also, the loss of the extremely dilated outer lip, as in *Dilatilabrum*, in *Persististrombus radix* and the subsequently regaining such a wing as present in many of the western Atlantic and Panamic fauna province species, seems unlikely.

However, a derivation of some Indo-Pacific species from a strombus radix-like species is not that unlikely. There are some morphological characters which link *bernielandui* Harzhauser, 2007, from the Oligocene late Chattian Warak formation, Gebel Madrasah, Oman, *S. gijskronbergi* Harzhauser, 2007 from the Miocene Aquitanian Gubbarah formation, Gebel Madrasah, Oman, *S. quilonensis* Dey, 1961 from the ?late Miocene of southern India and *Strombus pre-occupatus* Finlay, 1927 from the early to late Miocene of Java and Borneo (Indonesia) although the knobs are more strongly developed and much more spine-like.

reminiscent of *Strombus coronatus* and *Strombus latus*, and to some degree resembling *Persististrombus*.

Strombus preoccupatus was first assigned to *Lentigo* (as a subgenus) by Abbott (1960:123) but later (1965:402) transferred to *Dolomena* Wenz, 1940 (also as a subgenus). [*Dolomena* Iredale, 1931:212 is a *nomen nudum*, see Kronenberg & Dharma, 2005]. *Strombus sedanensis* Martin, 1899 of the early Miocene of Indonesia and Pakistan was assigned to *Dolomena* (as a subgenus) by Abbott (1960:102). This was followed by Raven (2002:13, pl. 5 fig. 26a, 26b) with *Dolomena* as a genus. In general shape *Strombus sedanensis* also reminds one of certain forms of *S. coronatus*, *S. latus*, and, to a lesser extent, as the outer lip of that species is clearly more dilated, *S. costatus*. Without providing an allocation for both these species, we reject the assignment of *S. sedanensis* to *Lentigo* (see remarks under description of *Persististrombus* gen. nov.) or *Dolomena*, because the structure of the outer lip clearly differs from species of that latter genus. Other species from the Miocene of Indonesia, such as *S. inflatus* Martin, 1879, *S. herklotsi* Martin, 1880, *S. tuberosus* Martin, 1883, *S. tjilonganensis* Martin 1899, as well as *S. mekranicus* Vredenburg, 1928 from the Miocene of Pakistan (all allocated to *Tricornis* by Abbott, 1960:61–62) should be critically re-examined in terms of their generic position and possible relation to the Recent and fossil Indo-Pacific species mentioned above. This task is beyond the scope of the present report.

Scenario 3)

The genus *Dilatilabrum* Cossmann, 1904 [TS *Strombus fortisi* Brongniart, 1823 from the Lutetian (middle Eocene) of Italy] may have been ancestral to (some of) the broad winged species. Species of *Dilatilabrum* are characterized by a widely-dilated outer lip (wing) and a large, narrow keel on the shoulder of the dorsal side of the body whorl. Based on the general shape and the presence of a keel-like ridge on the dorsum, both *S. dominator* Pilsbry & Johnson, 1917 from the Miocene of Santo Domingo, Dominican Republic and *S. dominator delabechei* Rutsch, 1931, known from the Pliocene Bowden Formation of Jamaica, could be assigned to *Dilatilabrum*, thus linking the Eocene *S. fortisi* to the Recent broad winged species. But *S. dominator* s.s. and *S. dominator delabechei* have a shallow strombid notch and a more or less clearly developed spiral sculpture on the latter part of the last whorl, both absent in *D. fortisi*. The large *D. roegli* (Harzhauser, 2001) [as *Strombus (Dilatilabrum) roegli*] from the Oligocene of Greece and Iran does have a strombid notch, but does not have the spiral sculpture present in *S. dominator* s.l.. Based on the consensus tree as presented by Latiolais *et al.* (2006:440) we do not think that the genus *Dilatilabrum* is closely related to the

modern fauna, and disappeared during the extinction wave at the end of the Eocene leaving only *D. roegli* to persist into the Oligocene, when it perished.

Savazzi (*vide* Harzhauser, 2001:58) suggests that the strombid notch evolved twice. Given the presence of the strombid notch in some other grades or clades of Stromboidea (Pugnelliidae; see remark by Kronenberg & Burger, 2002:43) and *Rimella*-like species, *Ectinochilus*, *Varicospira* and other genera (Clark & Palmer, 1923; Burger & Kronenberg, 2006), we suggest that this character may have arisen even more than twice.

Simone (2005: 248) used the absence of a strombid notch in Recent *Lobatus goliath* as a reversion in his listing of characters he used in his analysis. This strombid notch, however, is present in some specimens of *L. goliath*, and the absence of the notch in certain specimens is here considered not to be a reversion as argued by Simone (2005) but part of the intraspecific variation of this species.

The position of *Strombiconus* Marks, 1951 (TS *Strombiconus ecuadorensis* Marks, 1951, which is the only species ever assigned to this genus) from the Early Miocene of Ecuador is enigmatic. The two known specimens on which both the description of the species and the genus were based are juveniles with worn apices (Marks, 1951:141–142, pl. 9 figs 10–11), and the systematic position of this genus and species, although probably strombid, cannot be determined. The same is true for the more recently described *Austrombus* Nielsen, 2005 (TS *Comus medinae* Philippi, 1887) from the Miocene of Chile, as already acknowledged by Nielsen (2005:1122).

The overriding problem of convergence in the Strombidae impedes a morphological analysis of evolutionary relationships. An example is the resemblance between *Lobatus gallus* and *Tricornis tricornis* and the above-mentioned close resemblance of *Dilatilabrum* with some of the fossil and Recent Caribbean and Panamic species. What appears to emerge is a mosaic pattern of characters that appear, disappear and reappear between lineages, but also within one single lineage, see also Landau *et al.* (in prep.) We agree with Petuch (1994:258) that none of the American species should be assigned to *Tricornis* Jousseaume, 1886, which only superficially resembles certain of these American species.

Acknowledgments. We thank Dr. Alan G. Beu, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand, for making a copy of the paper by García-Talavera available; Dr. Eugene V. Coan, Palo Alto, California, U.S.A., for information on *Strombus obliteratus*; Dr. Yves Finet for information on Islas Galápagos references; William Frank of Jacksonville, Florida, U.S.A. for technical assistance in constructing the distribution map; Richard E. Petit, North Myrtle Beach, South Carolina, U.S.A., for sharing his opinion on the status of *Lobatus*; Han Raven, the Hague, the

Netherlands for the translation from Spanish; Dr. Geerat J. Vermeij, University of California at Davis, for critically reading the first draft of the manuscript and making valuable suggestions. Dr. Mathias Harzhauser, Naturhistorisches Museum in Wien, read the second draft of the manuscript and gave useful tips. An anonymous reviewer critically read the manuscript and made valuable remarks and suggestions. Bernard Landau, Albufeira, Portugal, is greatly acknowledged for making images of specimens of *P. radix* and *P. bouellii* available. The first author also wants to thank Adri W. Burger, Heerhugowaard, the Netherlands and Ron P.A. Voskuil, Hulst, the Netherlands for stimulating discussions, Dr. Mathias Harzhauser, Naturhistorisches Museum in Wien for kind hospitality and access to the collection in his custody, and finally Marianne Matthijssen for abiding support.

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